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Is escaping deer browse just a matter of time in *Picea sitchensis*? A chemical and dendroecological approach

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Abstract We combined chemical and dendroecological analyses to understand the mechanisms that are involved in escaping deer browse by young Sitka spruce (*Picea sitchensis*) exposed to browsing by Sitka black-tailed deer (*Odocoileus hemionus sitchensis*) on Haida Gwaii (British Columbia, Canada). We compared chemical defences (terpenes), nutritive compounds (nitrogen, non-structural constituents, cellulose, and lignin), as well as age and radial growth of two young spruce categories growing side by side: (1) stunted spruces that were heavily browsed, shorter than the browse line, and (2) escaped spruces that were taller than the browse line but still browsed below the browse line. Escaped and stunted spruces did not differ in terpene concentrations, or in nutritive compound contents, suggesting that they had similar palatability. Escaped spruces were older than stunted spruces. Stunted and escaped trees had similar slow growth when young, suggesting no difference in initial browsing between the two spruce categories. For escaped spruce, there was a dramatic increase in radial growth at about 12–13 years old, suggesting that the apex of the trees had escaped deer browse. Because the two categories of spruces were equally accessible and did not differ in chemical defences or in nutritive compounds, and because escaped spruces were older than stunted trees and had a similar slow radial growth in their first 12–13 years, we conclude that morphological differences between stunted and escaped browsed trees are due to age and that it is only a matter of time before spruce escape deer on Haida Gwaii.

Keywords *Picea sitchensis* (Bong.) Carrière · Deer browsing · Chemical defences · Radial growth · Age

Introduction

Herbivory can trigger changes in plant morphology (Bergström and Danell 1987; Duncan et al. 1998), growth (Chouinard and Filion 2001; Rolland et al. 2001), or chemical defences (e.g. Bryant et al. 1991; Tuomi et al. 1991; Garabini et al. 2001). These changes, in turn, can affect the probability and magnitude of future herbivory (Machida 1979; Duncan et al. 1998) by the increase or the decrease (i.e. the trigger of induced defences) of plant palatability. In conifers, insect herbivory or mechanical wounding can induce chemical defences (Marpeau et al. 1989; Lerdaun et al. 1994; Litvak and Monson 1998). However, because evergreen species usually store more of their carbon and nutrient reserves in leaves than do deciduous trees (Chapin 1980), severe and repetitive defoliation of evergreens by mammal herbivores can reduce carbon available for defence chemicals and increase their palatability (Bryant et al. 1983; Raffa and Smalley 1995). Therefore, when morphological differences are observed among individuals submitted to the same browsing pressure, it is difficult to determine what causes this variation. In conifers, the variation can be the result of different mechanisms. First, it could reveal a difference in browsing history caused by initial variation in browsing intensity by the herbivore that was not linked to a plant's palatability. This initial variation could be due, for example, to unequal plant accessibility, random herbivory, or neighbouring plants (Hjältén and Price 1994; Gómez et al. 2001). Second, there could be a genetic variation in defence production of the trees that leads herbivores to browse preferentially less defended genotypes. Finally, morphological differences could underline age differences between trees for two reasons:

1. Plant defence may vary with ontogeny resulting from developmental constraints or stronger selection for

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defence against herbivores and pathogens at the juvenile rather than the adult stage (Kearsley and Whitham 1989; Bryant and Julkunene-Tiitto 1995; Karban and Thaler 1999; Swihart and Bryant 2001).

2. Because browsing can slow down tree growth, small browsed trees could simply be younger than trees that escaped deer browse by growing above deer reach.

One approach to reveal the source of browsing variation observed in the field would be to conduct a common garden experiment with controlled herbivory and developmental factors. For long-lived species such as conifers, however, time constraints are usually impediments to using this technique. Our approach was to combine dendroecological and chemical analyses. The chemical analysis gives information about tree palatability in terms of secondary metabolites and nutritious compounds. Dendroecological analyses yield data on tree age, growth pattern, growth rate and growth morphology. With proper sampling, differences in growth patterns of trees growing at the same sites can be attributed to biotic factors, such as herbivory, as opposed to abiotic factors such as climatic variation (Chouinard and Filion 2001).

We conducted our study on Sitka spruce [*Picea sitchensis* (Bong.) Carrière] on Haida Gwaii (British Columbia, Canada) where Sitka black-tailed deer (*Odocoileus hemionus sitchensis* Merriam) place heavy browsing pressure on its regeneration (Pojar et al. 1980; Coates et al. 1985). In sites where spruces are all accessible to deer, some trees remain within the height of deer browsing while others are able to grow beyond browsing height. In order to understand the causes of this variation, (1) we determine whether there was a difference in palatability between the two tree categories looking at defensive secondary compounds and nutritional compounds, and (2) we analyse the relation between plant age, radial growth and herbivory history in the two tree categories using dendroecology.

Materials and methods

Study area

The Haida Gwaii archipelago (53° N, 132° W), situated on the Pacific coast of Canada in British Columbia, is composed of more than 150 islands (Fig. 1). The Islands of Laskeek Bay, where trees were sampled, are located on the eastern side of the archipelago, which corresponds to the Coastal Western Hemlock Zone, wet Hypermaritime sub-zone (CWHwh). At this low elevation, old-growth forests consist of a mixture of Sitka spruce, western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and western red cedar (*Thuja plicata* Donn). The understory is composed of shrubs such as salal (*Gaultheria shallon* Pursh), red huckleberry (*Vaccinium parvifolium* Smith in Rees), grasses, mosses and lichens (Banner et al. 1989).

Plant material and sampling

Sitka spruce

Sitka spruce is a major component of North America's north temperate coastal rain forest (Peterson et al. 1997). It is the second conifer preferred by deer after western red cedar in the CWHwh

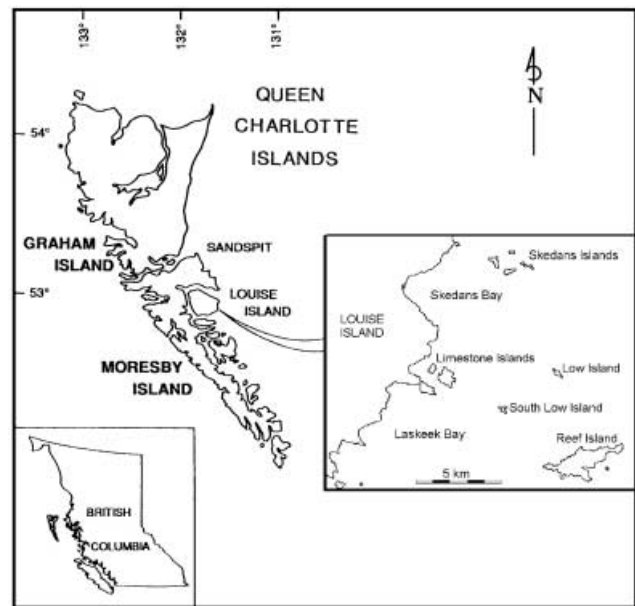


Fig. 1 Haida Gwaii archipelago in British Columbia (Canada) with East Limestone Island and Reef Island where spruces were sampled

zone of Haida Gwaii (Pojar et al. 1980; Martin and Daufresne 1999) and it may become an alternative food source, where western red cedar regeneration has been severely reduced by deer browsing (Pojar et al. 1980). Large, commonly up to 70 m tall, it is a shade-intolerant, submontane to montane evergreen conifer occurring in hypermaritime to maritime mesothermal climates on nitrogen-rich soils (Pojar and MacKinnon 1994).

Sampling site

Sampling was carried out in May 1999 at two sites. One was a windthrow of East Limestone Island (49 ha) and the second a windthrow on Reef Island (249 ha) in Laskeek Bay. On East Limestone Island the windthrow corresponded to the death of an old central big spruce and was characterized by a slope of ca. 3° and a badly drained 300° exposure. Organic soil was 50 cm thick. Surrounding trees were spruces and western red cedars. On Reef Island, the surrounding canopy comprised a majority of spruces and a few hemlocks. The site was characterized by a slope of ca. 24° and a 200° exposure. It was well drained and had a 60 cm layer of organic soil. At both sites, regeneration consisted exclusively of spruce, the canopy was open and the light conditions were good.

Deer density estimation was ca. 0.30 deer/ha on Limestone Island (Daufresne 1996). On Reef Island, where density was similar, a deer eradication program started in October 1997 and has been maintained since then to keep deer populations below 10 individuals. The absence of a shrub layer, the scarcity of ground vegetation, the confinement of palatable species to inaccessible areas, and the existence of a browse line indicate very heavy browsing pressure (Reimoser et al. 1999) on Limestone and previously on Reef Island. The browse line is the maximum height at which deer can browse the trees. For Sitka spruces, this limit is extremely constant compared to other species because the stem is difficult to bend. On Haida Gwaii it has been shown to be 1.16 ± 0.07 m (Vila and Guibal 2002). This browse line differs according to species and can reach 1.50 m (Martin and Daufresne 1999).

Sampling criteria

We sampled the two tree categories that were found in the wind-throws:

1. Stunted spruces that were non-mature trees that displayed a shrubby, bonsai-like morphology, and that were shorter than the browse line (Fig. 2). The typical shape of these trees resulted from activation by browsing of dormant buds from secondary axes or from lower levels, which caused intense ramification (Vila and Guibal 2002).
2. Escaped spruces that were non-mature trees that had grown above the browse line but were shorter than 4 m. Escaped spruces display a shrubby stunted port shape below the browse line and resumed a normal shape above (Fig. 2).

In order to warrant that trees were equally accessible to deer, we sampled trees in pairs with less than 20 cm between branches from stunted and escaped trees within each pair. Fifteen pairs were sampled on each island.

Plant chemical composition

For chemical analyses, we sampled current-year needles that were at the end of the stem, on stems that were below the browse line. At the time of the sampling new needles were still in closed buds. We analysed chemical composition using two techniques:

1. Gas chromatography (GC) on methanol extracts made from fresh leaves to analyse mono- and diterpene content. Terpenes are abundant in conifer leaves (Banthorpe and Charlwood 1980; Bohlmann and Croteau 1999; Trapp and Croteau 2001) and Sitka spruce monoterpenes have been shown to be negatively correlated with red deer (*Cervus elaphus*) food choice (Duncan et al. 1994).
2. Near infrared reflectance spectroscopy (NIRS) to determine leaf content of nitrogen, non-structural constituents, hemicellulose, cellulose and lignin.

GC analysis

Three grams of fresh leaf material from each plant sample were extracted with 30 ml methanol for 48 h. After filtration the extracts were stored at -20°C until analysed for terpene content by gas chromatography. Extracts were analysed on a Hewlett Packard (model 6890) gas chromatograph equipped with a flame ionization detector and a 30 m x 0.25 mm 5% phenyl methyl siloxane column (Hewlett Packard); He flow = 2.5 ml/min (38 cm/s); injector and detector temperatures = 200°C and 300°C respectively; the temperature program was 50°C for 2 min, ramped to 280°C at $10^{\circ}\text{C}/\text{min}$ and then held at 280°C for 5 min. Assignments of chromatographic peaks were made by similar chromatographic analysis using a Hewlett Packard (model 5972) mass selective detector and subsequent computer matching of the mass spectra with library spectra.

NIRS study of leaf chemical composition

All the samples were dried in a forced-convection oven at 55°C for 24 h, ground in a cyclone mill (Cyclotec Sample Mill, Tecator) through a mesh of 1-mm aperture diameter, and subsequently scanned with a near-infrared reflectance spectrophotometer (NIR-Systems 6500). Two replicate measurements of monochromatic light were made at 2-nm intervals over a range from 400 to 2,500 nm, to produce an average spectrum with 1,050 data points. Reflectance (R) was converted to absorbance (A) using the following equation: $A = \log(1/R)$. Data analysis was conducted using the ISI software system (Shenk and Westerhaus 1991a).

NIRS has become widely used as a rapid, accurate and low-cost method for measuring the chemical composition of plant and animal tissues (Foley et al. 1998). In particular, this method has been used recently and successfully for measuring forest foliage composition

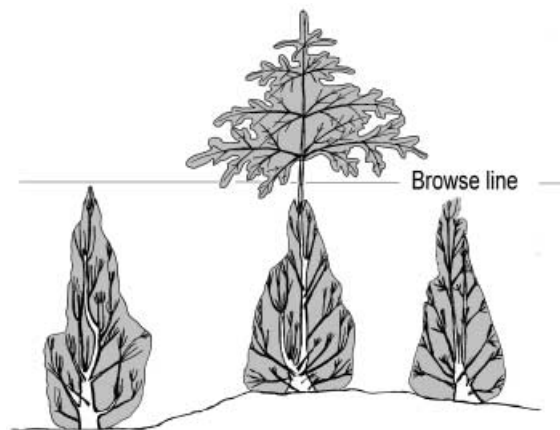


Fig. 2 Schematic representation of stunted spruces that are heavily browsed and shorter than the browse line, and escaped spruces that have exceeded the browse line. Escaped spruces display a stunted shape under the browse line and a normal shape above. For Sitka spruce, the browse line, which is the greatest height at which deer can browse the tree, is at 1.16 ± 0.07 m

(Martin and Aber 1994; Bolster et al. 1996; Gillon et al. 1999). NIRS uses reflectance signals resulting from bending and stretching vibrations in bonds between carbon, nitrogen, hydrogen, and oxygen. Calibration is the process of deriving spectrochemical models that relate the spectra of samples to their laboratory reference values (Shenk and Westerhaus 1996). Calibration equations had been previously monitored for nitrogen, hemicellulose, cellulose, lignin and ash from large sets of ligneous foliage samples (187–369 samples of 28 species including several conifer species) according to the method described by Shenk and Westerhaus (1991b), Joffre et al. (1992), and Gillon et al. (1999). To make sure that these calibration equations could be used for our spruce samples, we first checked that spruce samples belonged to the same spectral populations as the calibration sets. Mahalanobis distances (H) (Mahalanobis 1936) of spruce samples to the average spectra of the calibration sets were then computed. It is generally assumed that the samples whose spectra have an H value of >3 are outliers compared to the population (Shenk and Westerhaus 1991b). All our 60 spruce samples had H values <3 , except for 2 samples ($H = 3.02$ and 3.25) compared to the calibration set for hemicellulose and 4 samples (H from 3.15 to 3.49) compared to the calibration set for cellulose. Mean H of our 60 spruce samples to the average spectra of the different calibration sets ranged from 1.11 to 2.28. Consequently, the calibration equations that were already established could be applied to our spruce samples. We then used these calibration equations to determine concentrations in ash with standard error of calibration of 0.55%, nitrogen (0.10%), hemicellulose (1.74%), cellulose (0.99%), and lignin (1.24%). We then calculated the percentage organic matter ($\text{OM} = 100 - \text{ash}$) and the non-structural constituents [$\text{NSC} = \text{OM} - (\text{hemicellulose} + \text{cellulose} + \text{lignin})$] of all spruce samples.

Statistical analysis

Terpenes

We calculated the concentration in dry matter of each monoterpene per tree and used a square root and arcsine transformation to normalize the data (Sokal and Rohlf 1981). We considered every terpene concentration to be a quantitative response variable and used a multivariate analysis of variance (MANOVA) (SAS 1999) with site (Limestone and Reef) and category (escaped and stunted) as explanatory variables. We identified the significant response variables using ANOVA (SAS 1999) and corrected the level of significance, α , by the improved Bonferroni procedure for multiple tests

proposed by Simes (1986). The method arranges the P -values $P_{(1)}, \dots, P_{(n)}$ in increasing order for testing hypotheses $H_0 = [H_{(1)}, \dots, H_{(n)}]$. H_0 is rejected if $P_{(j)} \leq j\alpha/n$ for any $j=1, \dots, n$, so that corrected $P_{c(j)} = P_{(j)}n/j$ can be compared to α . Means and standard errors were calculated by LSMEANS in the GLM procedure (SAS 1999).

Chemical composition

We considered every NIRS predicted chemical constituent to be a quantitative response variable and used MANOVA (SAS 1999) with the same "site" and "category" qualitative explanatory variables. We identified the significant response variables using ANOVA. Levels of significance were corrected by the improved Bonferroni procedure as used for terpenes.

Dendrochronology

We sampled either stem cores with a Swedish increment borer or, when the stem diameter was too small, stem cross-sections. Cores and cross-sections were sampled at the bottom of the stem, just above the collar. For each tree, coring was repeated until pith was reached in order to obtain the longest ring series, which is necessary to establish the age of the tree.

To analyse ring series and determine tree age, tissue structure was made visible by polishing the sample transversal section with sandpaper of different grades. In order to accurately date each ring, we proceeded to tree ring cross-dating (Fritts 1976). Cross-dating is based on identifying similar ring sequences that have the same characteristic features on different samples. For each tree, age was determined by counting rings on basal cross-sections or cores. Age differences were analysed by ANOVA (SAS 1999) with category and site as the qualitative explanatory variables.

Once rings had been dated, we chose suitable radii to measure ring widths that avoided irregularities. Cross-sections were measured along two radii (1/100 mm) using an Eklund measuring device. The average value of each ring width was calculated in order to obtain individual chronology for each spruce (Fritts 1976; Cook and Kairiukstis 1990). We analysed variation in growth ring width with age using a repeated measure time analysis with age as a time factor (SAS 1999). Because trees were not necessarily the same age, we used the age range where at least all trees but three per category occurred. We tested the effects of age, age \times category, age \times site and age \times category \times site. We used multivariate (MANOVA) as opposed to univariate (ANOVA) analyses to avoid data circularity problems and because some of the sample sizes were unbalanced (Von Ende 1993). We used analysis of variance of contrasts in order to identify changes in ring width between two consecutive ages. If escaped and stunted spruces differed in age, we did a repeated measure time analysis within each category.

Finally, we graphed escaped and stunted spruces' ring width according to time in order to achieve an overview of the changes with time.

Results

Plant chemical composition

Terpene analyses

We focused on the eight major terpene peaks (five monoterpenes and three diterpenes) present in most of the samples. Two peaks were identified as β -myrcene and the mixture of limonene and β -phellandrene.

The MANOVA on the terpene concentrations revealed that the category effect was not significant ($F_{8, 49}=1.191$, $P=0.324$) but the site effect was ($F_{8, 49}=4.445$, $P<0.001$). The category \times site interaction was not significant ($F_{8, 49}=0.858$, $P=0.558$). Concentrations of four monoterpenes and one diterpene were significantly higher on Reef than on Limestone Island (Fig. 3).

Biochemical composition

MANOVA of the five NIRS-predicted chemical constituents showed a significant interaction between site and category (Table 1). Therefore, for each site, we ran a MANOVA with category as the explanatory variable. The effect of category on the leaf chemical composition was significant for spruces on East Limestone but not on Reef Island (Table 1). However, the slight differences

Fig. 3 Means with standard error bars of mono- (A–E) and diterpene (F–H) concentrations in stunted and escaped Sitka spruce on Reef and Limestone Islands. Stars (*) indicate the P values (corrected by the improved Bonferroni method, see text) for the comparative foliage concentrations between trees on Reef and Limestone Island. Differences between escaped and stunted trees are not significant. * $P_c<0.05$, ** $P_c<0.01$

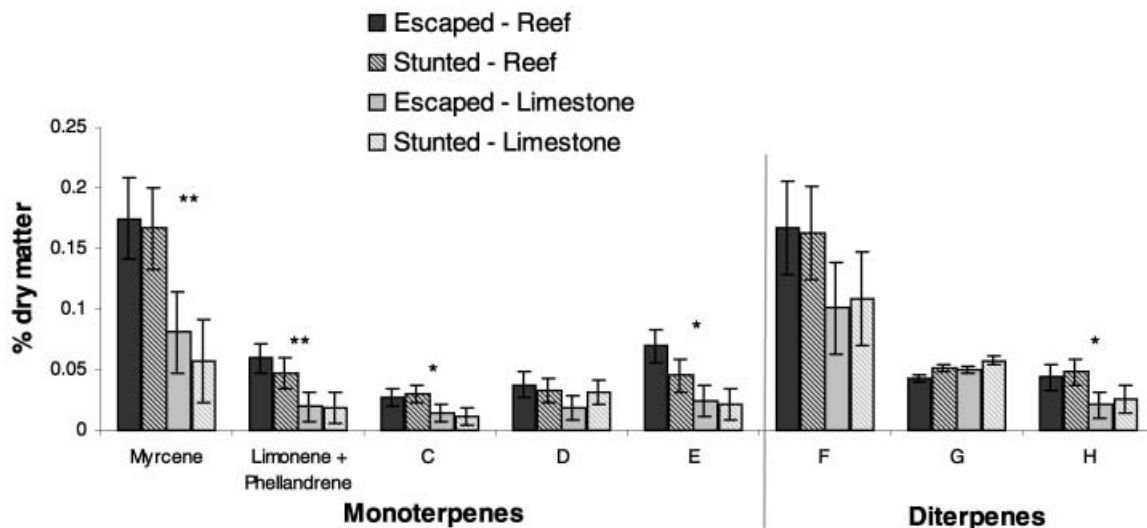
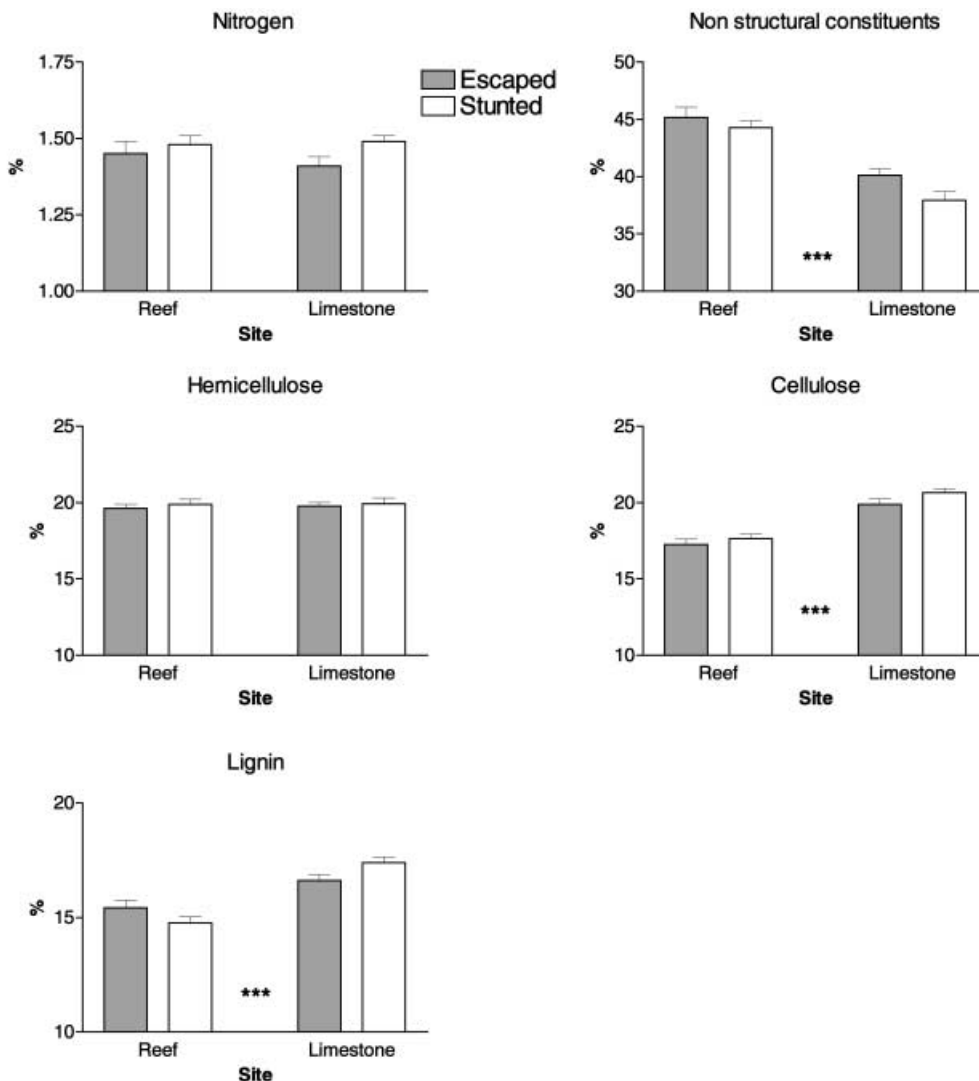


Table 1 Results of the MANOVA on escaped and stunted spruce foliage nutritive compound content (nitrogen, non-structural constituents, hemicellulose, cellulose, and lignin). Spruces were sampled on East Limestone and Reef Islands on Haida Gwaii. (*Num DF* numerator degree of freedom, *Den DF* denominator degree of freedom)

Data set	Effect	Roy's greatest root	F value	Num DF	Den DF	P>F
All samples	Site×category	0.34	3.50	5	52	0.008**
	Site	1.56	16.23	5	52	<0.001***
	Category	0.19	2.03	5	52	0.090
Reef	Category	0.50	2.38	5	24	0.069
Limestone	category	0.92	4.43	5	24	0.005**
Escaped	Site	1.16	5.61	5	24	0.002**
Stunted	Site	3.27	15.68	5	24	<0.001***

Fig. 4 Mean concentrations with standard error bars of nutritive compound content in foliage of escaped and stunted Sitka spruces sampled on Reef and Limestone Islands on Haida Gwaii. Stars (*) indicate the P values (corrected by the improved Bonferroni method, see text) for the comparative foliage concentrations between trees on Reef and Limestone Island. Differences between escaped and stunted trees are not significant. *** $P_c < 0.001$



measured on Limestone Island (higher concentrations in non-structural constituents in the escaped spruces and lower concentrations in lignin) were not significant after the Bonferroni corrections. The site effect was significant in the MANOVA for both categories (Table 1). On Reef Island foliage was richer in non-structural constituents and poorer in cellulose and lignin than on East Limestone, for both escaped and stunted trees (Fig. 4).

Dendrochronology

Of the 30 paired spruces selected for chemical analyses and sampled for dendroecological analyses, the radial growth of one stunted and two escaped spruces on Limestone Island and one stunted and one escaped spruces on Reef Island could not be measured because of stem deformation at the collar.

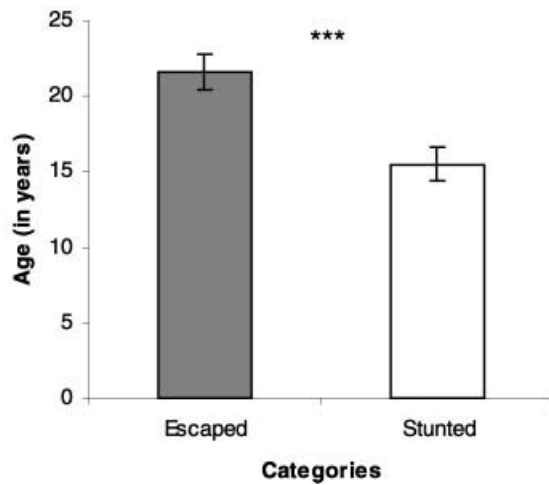


Fig. 5 Mean ages with standard error bars of stunted and escaped spruces on Reef and Limestone Islands of Haida Gwaii. Age differences between escaped and stunted spruces are significant: *** $P_c < 0.001$

Age

The ANOVA on tree age revealed that the category effect was significant ($F_{1, 52} = 13.85$, $P < 0.001$). Stunted spruces (13.93 ± 4.60 years on Reef Island, 16.93 ± 6.07 years on Limestone Island) were significantly younger than escaped spruces (20.64 ± 5.54 years on Reef Island,

22.00 ± 7.16 years on Limestone Island) (Fig. 5). The site effect ($F_{1, 52} = 2.39$, $P = 0.130$) and the site × category interaction were not significant ($F_{1, 52} = 0.14$, $P = 0.713$).

Radial growth pattern

Because 1st-year rings were sometimes missing or deformed, we did not include them in the analyses. For the multivariate repeated-measure analyses with all the trees, we considered ages from 2 to 9 years. We found a significant effect of age but not of age × category, age × site or age × site × category (Table 2). Ring width increased with age (Fig. 6). Since escaped trees were older than stunted trees, we did a repeated measure time analyse separately for each category with site as a explanatory variable. For stunted trees the overall effect of age analysed from 2 to 9 years old was significant [Roy's greatest root (RGR) = 1.690, $F_{7, 16} = 3.86$, $P = 0.012$]. There were no changes in ring width between two consecutive ages as no contrasts were significant (all $P < 0.05$). The age × site effect was not significant (RGR = 0.260, $F_{7, 16} = 0.59$, $P = 0.753$). For escaped trees, we analysed the effect of age from 2 to 15 years, which was significant (RGR = 8.512, $F_{13, 8} = 5.24$, $P = 0.012$). Changes in ring width were significant between age 4 and 5 years ($F_{1, 20} = 4.91$, $P = 0.038$), age 8–9 years ($F_{1, 20} = 7.41$, $P = 0.013$), and age 12–13 years ($F_{1, 20} = 8.84$, $P = 0.007$) (Fig. 6). The age × site effect was not significant (RGR = 1.530, $F_{13, 8} = 0.94$, $P = 0.557$).

Fig. 6 Mean ring widths (with standard error bars) according to age of stunted and escaped spruces on Reef and Limestone Islands of Haida Gwaii. Data shown correspond to age where less than three individuals by category are missing. Stars (*) show significant increase in ring width between two consecutive ages for escaped trees: * $P_c < 0.05$, ** $P_c < 0.01$

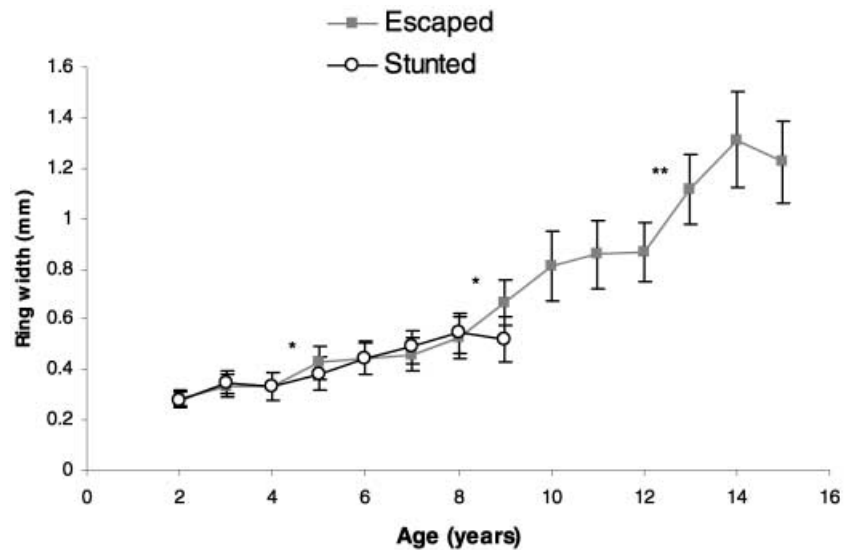


Table 2 Repeated measure time analysis of variance of ring width series using age as time factor, done on escaped and stunted spruces growing on Reef and Limestone Island on Haida Gwaii. (Num DF numerator degree of freedom, Den DF denominator degree of freedom)

Effect	Roy's greatest root	F value	Num DF	Den DF	P
Age	0.858	4.66	7	38	<0.001***
Age × category	0.296	1.61	7	38	0.163
Age × site	0.130	0.71	7	38	0.666
Age × category × site	0.073	0.40	7	38	0.898

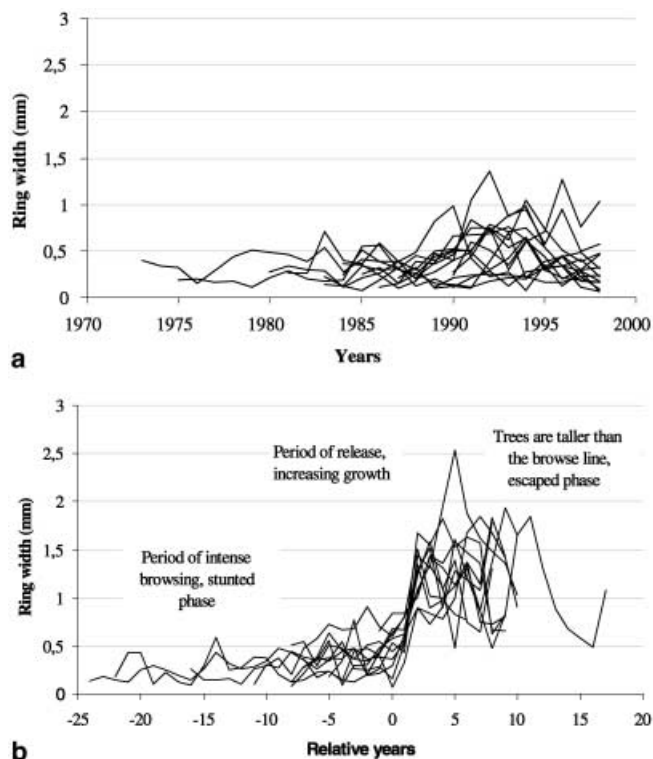


Fig. 7 Radial growth chronologies showing the typical variation in ring widths with time in (a) stunted spruces and (b) escaped spruces sampled on Limestone Island on Haida Gwaii. Time is given in relative years where year 0 corresponds to the first year of 4 consecutive years with 2–3 times increase in ring width

Stunted spruces were characterized by a regular increase in ring width that remained between 0.2 and 1 mm (Figs. 6, 7a).

The ring sequences of escaped spruces were characterized by three periods (Fig. 7b): (1) a period when ring width was less than 1 mm that lasted approximately 12–13 years; (2) a 1- to 2-year period when ring width increased by 2- to 3-fold up to 2.5 mm; and (3) a final period with stabilized growth. The age at which the sharp increase in growth occurred was 11.77 ± 4.08 years for escaped spruces on Reef Island and 13.33 ± 5.94 for spruces on East Limestone Island.

Discussion

Escaped and stunted spruces did not differ in terpene concentrations, and thus monoterpenes seem not to be involved in the differential browsing observed, a contrary conclusion to that of other studies (Duncan et al. 1994; Jason et al. 1996). There were no differences in nutritive compounds (nitrogen, non-structural constituents, cellulose, and lignin) between escaped and stunted trees on Reef Island and differences were small on East Limestone Island. Thus, the two spruce categories did not differ in terms of chemical palatability. Another factor that could influence palatability is needle thorniness.

However, this point has not been mentioned much in the literature that has examined factors influencing palatability of spruce to cervids (Duncan et al. 1994, 1998, 2001; Jason et al. 1996;). Furthermore, no difference in fibres (lignin and cellulose) that could be indicative of needle toughness occurred between the two categories. Therefore, because escaped spruces were still browsed below the browse line, our results suggest that the palatability of escaped and stunted spruces' did not differ, nor did their browsing shape influence their chemical defence and nutritive quality. This confirms the findings of Duncan et al. (1998), who showed that chemical composition of Sitka spruce was not affected by red deer browsing. Consecutively, morphological differences between escaped and stunted spruces cannot be explained by the existence of genetic variation in chemical defence potential.

The facts that radial growth was similar in escaped and stunted trees when they were young and that ring width tended to increase slightly with age in both categories suggest that both tree categories underwent intense browsing pressure at the beginning of their life. Similar observations on ring series have been made by Schweingruber (1996) on deciduous trees browsed by domestic herbivores.

For the older escaped trees, however, we observed a drastic increase in ring width around 12–13 years old with high growth maintained thereafter. This suggests that an apical bud had reached the browse line and started to escape deer at that time. The reaching of the browse line by apical buds can be explained by the fact that, when buds and needles are pulled off by deer, a small piece of the new stem and a few needles usually remain attached to the trees (authors' observations). The repetition of this process year after year allows the trees to slowly grow in height with the typical cushion shape to eventually reach the browse line (Vila and Guibal 2002). In a common garden experiment Duncan et al. (1998) showed that previous browsing had a considerable impact on tree morphology.

With the radial growth pattern, we determined that escaped spruces took about 12–13 years to reach the browse line. According to Coates et al. (1985) who showed on Haida Gwaii archipelago that protected spruces need only 5 years to reach a height of 1.18 m, we conclude that browsing by deer delays saplings' growth by at least 7–8 years at deer densities such as those documented for the two study sites. Escaped spruces that reached the browse line about 10 years ago had a similar age to stunted trees that are still smaller than the browse line by 0.3–0.4 m today. This suggests an increase in browsing pressure over the last 15 years.

Difference in chemical composition occurred between sites. On Reef Island, needles were richer in terpenes, non-structural constituents, and poorer in fibres than on Limestone Island. This could reveal better growing conditions on Reef than on East Limestone Island. Duncan et al. (1998) already underlined that foliage chemical composition may be altered by the effect of the underlying

ing soil type on growth rate. The chemical differences in foliage between the two sites could also arise from the fact that spruces on Reef Island did not undergo heavy browsing pressure in 1998 because of the deer eradication that occurred at the end of 1997. Browsing release can allow trees to produce more foliage and allocate more resources to defence.

Because (1) spruces were all equally accessible, (2) no difference in chemical defences or nutritive compounds was found, (3) stunted trees were younger than escaped trees, but (4) escaped trees showed a similar low growth pattern in their first growth phase, we conclude that morphological differences between stunted and escaped browsed trees are due to age, and that it is only a matter of time before spruce escapes deer on Haida Gwaii. This is not true for all species; some less resistant to browsing pressure die before they reach the browse line for similar deer densities. For example, on Haida Gwaii heavily browsed and lightly browsed western red cedar do not differ in age, but lightly browsed trees seem to have a better genetic potential for defences. Resistance of spruce to browsing is principally explained by the presence of dormant buds, which can be activated after shoot loss (see Gill 1992). A parallel can be made with the "hide-and-resprout strategy" of some tree species to savannah fire (Gignoux et al. 1997). Savannah fires affect mostly tree recruitment and not adult survival, as adults are resistant to flames that are mostly in the herbaceous strata. This is similar to browsing by ungulates affecting mostly young trees (Kearsley and Whitham 1989, Swihart and Bryant 2001). To recruit into the adult population, young trees must accumulate enough underground structure between two successive fires, to produce a trunk that is higher than the herbaceous level, and resistant to fire. In the same way, spruces have to produce enough stems each year in order to be able to top the browse line between two successive browse attacks.

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